

Food Requirements and Sources for Juvenile Atlantic Menhaden

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Abstract

The role of juvenile Atlantic menhaden *Brevoortia tyrannus* in the energetics of the estuarine and nearshore ecosystem along the Atlantic coast of the United States is unknown, though hypothesized to be significant. Our objectives were to summarize existing data on feeding rates of individual fish and on population size, and to combine them to produce a preliminary estimate of the food required by the population of juveniles. Estimates of the total food consumed by each fish during its residency in the estuary ranged from 21.5 to 32.7 g dry weight of organic matter. Three population estimates ranged from 4.4×10^9 to 11.2×10^9 fish present in the autumn. An assumed average of 8.5×10^9 Atlantic menhaden would consume from 183×10^6 to 278×10^6 kg of organic matter, which is 6-9% of estimated phytoplankton production. The population's estimated daily consumption in the autumn ranges from 0.6 to 1.0 g/m², which equals the average daily phytoplankton production of 0.8 g/m². We conclude that the population of juvenile Atlantic menhaden may consume more food during its residency than is available from phytoplankton or a phytoplankton-based food chain. Organic detritus is suggested as an alternate source of energy.

The vast Atlantic menhaden *Brevoortia tyrannus* populations that occur in the Atlantic and Gulf of Mexico coastal waters have been the subject of numerous fishery investigations. Both fishing pressure and environmental factors contribute toward considerable changes in stock size (Schaaf and Huntsman 1972; Schaaf 1975; Nelson et al. 1977). Any change in abundance undoubtedly causes additional changes and adjustments in material and energy flow through coastal ecosystems, and may affect the population size and dynamics of Atlantic menhaden predators and competitors. The Atlantic menhaden's role in the flow of energy through the estuarine ecosystem may be complex because of such factors as unequal age distribution within the population and extensive coastal migrations, but it must be understood if we are to achieve the most effective recreational and

commercial utilization of living estuarine resources.

Our objective was to estimate the rate of energy flow through the population of juvenile Atlantic menhaden. A deterministic model presented here is intended (1) to arrange current facts and hypotheses about the population of juvenile Atlantic menhaden and its environment in a systematic fashion; (2) to check for contradictions in available data; and (3) to determine if the facts presented contribute insight to the functioning of the estuarine ecosystem. Information on the rates of ingestion, respiration, and growth of individual fish is combined with population estimates in order to estimate food utilization rates of all juveniles. Most of the data are from the literature, though some new data are presented.

The analysis suggests that the population of

juvenile Atlantic menhaden may use more food than is available from phytoplankton or from a phytoplankton-based food web; organic detritus may be a major source of food and energy.

Energy Requirements of Individual Fish

Estimates of the amount of energy used by individual Atlantic menhaden can be based on measures of metabolic requirements, estimates of daily ration determined from feeding studies, and calculation of the amount of food required to sustain estimated growth rates. Because of inconsistencies and suspected biases in the first two methods, which we discuss later, we chose to estimate daily ration from the growth-rate data:

$$\text{ingestion} = \text{growth rate} \div \text{gross growth efficiency.}$$

Natural growth rates were calculated from seasonal changes in average weight of juveniles from three estuaries. In 1969 larval recruitment in White Oak River, North Carolina, ended by mid-April. These fish grew at an average daily compound rate of 5.8%, from 65 mg on April 16 to 700 mg 41 days later, when the fish were so large that net avoidance became significant (Lewis et al. 1972). Juveniles in White Creek, Delaware, grew from about 0.6 g in early June to 17.6 g by late August 1957, for a daily growth rate of 3.8% (A. L. Pacheco and G. C. Grant, National Marine Fisheries Service, Beaufort, unpublished data). During 1971 in Newport River, North Carolina, juveniles grew from 1.1 g to 24.2 g in 82 days, a daily growth rate of 3.8% (length data from Kroger et al. 1974; length-weight relationship from Schaaf and Huntsman 1972).

The size-related change in estimated growth rate for Atlantic menhaden in the three estuaries, about 6%/day for small juveniles and 4%/day for larger ones, agrees with other available information. The average date for Atlantic menhaden larvae entering White Oak River, North Carolina, is approximately March 1 (Wilkins and Lewis 1971). From a mean size of 20 mm or 0.015 g at this time (W. R. Nelson, National Marine Fisheries Service, Beaufort, personal communication), a growth of 5.8%/day would bring them to 1.1 g by mid-May. Working nearby in Newport River, Kroger et

al. (1974) found that fish averaged 44 mm (1.1 g) on May 24. Thus, a daily growth rate of about 6% for small juveniles seems reasonable. Growth of larger juveniles (>1 g) during the summer was the same in both North Carolina and Delaware (3.8%/day). Summer growth rate declines as the fish get larger and the water cools, yet it produces fish weighing approximately 60 g by autumn (Kroger et al. 1974).

The 60-g estimate by Kroger et al. (1974) for fall juveniles came from fish blocknetted in an experimental cove. It is greater than the average size of juveniles caught in the North Carolina fall fishery, which is about 40 g (Reintjes 1969). This discrepancy may be due to especially favorable growing conditions in the experimental cove. Alternatively, it could be due to an influx of smaller juveniles into the North Carolina autumn fishery from the north, where spawning is delayed later into the spring; such a migration has been documented by tagging studies (Kroger et al. 1971). In light of the unquantified migration of northern juveniles into the North Carolina fishery and the sensitivity of final weight to small changes in daily growth rate, the size of fish caught in the autumn fishery does not refute our previous calculations that growth rate of juveniles approaches 4%/day.

Although gross growth efficiency (the fraction of organic matter ingested that is converted to new growth) has not been determined for juvenile Atlantic menhaden, it can be estimated from other information. Larval Atlantic menhaden feeding on *Artemia* sp. in the laboratory at natural temperatures attained efficiencies of approximately 30% (D. S. Peters, M. T. Boyd, and J. C. DeVane, National Marine Fisheries Service, Beaufort, unpublished data). As Atlantic menhaden grow from larvae to juveniles, their diet changes from animal matter to plant material; we can expect a corresponding increase in the amount of crude fiber ingested and a consequent reduction in growth efficiency. Although the efficiencies that occur in nature will be influenced by a variety of factors including diet composition, ingestion rate, and environmental conditions (Hastings and Dickie 1972; Peters and Kjelson 1975), data from other species can serve as a reasonable guide. Welch (1968) presented data on 29 aquatic organisms for which the average gross growth efficiency was 21%. Because the growth effi-

TABLE 1.—*Estimate of the total organic matter consumed by an Atlantic menhaden during growth from 0.015 to 30 g wet weight.*

Growth increment in dry weight (live weight)	Daily growth rate	Growth efficiency	Daily ration ^a	Grams organic matter consumed ^b
0.003–0.2 g (0.015–1.0 g)	6%	40% 30%	0.15 0.20	0.5 0.7
0.2–6.5 g (1.0–30 g)	4%	30% 20%	0.13 0.20	21 32

^a Organic matter expressed as a fraction of dry body weight.

^b Organic matter consumption = (net growth in dry weight) ÷ (growth efficiency).

ciencies of Atlantic menhaden in nature are not known, we used several efficiency values in calculating estimated food ingestion rates. With efficiencies ranging from 20% to 40% the calculated daily ration of organic matter ranges from 13% to 20% of dry body weight (Table 1). The higher efficiencies (40% for larvae and 30% for juveniles) probably exceed natural levels and thus give a conservative estimate of ingestion rate.

Other possible methods of estimating daily ration include the energy-balance approach (addition of growth, respiration, excretion, and egestion) and more direct measurements from feeding studies (for example, gastrointestinal evacuation). We have an estimate of respiration rate (Hettler 1976) that is equivalent to about 3% of dry body weight per day. This added to an average growth rate of 5% yields a minimal daily ration equal to approximately half the estimates in Table 1. The energy-balance estimate is obviously low because it does not include egestion and excretion, for which we have no estimates, and also because the respiration rate does not include energy required for feeding. Daily ration also might be estimated by the evacuation technique (Bajkov 1935). Based on information by Peters and Kjelson (1975), we can derive an estimated organic daily ration of about 5%. Because this value is less than just estimated growth plus respiration, we rejected this technique. It is well known that Bajkov's method is quite sensitive to estimates of the evacuation rate constant, and we think variations in food quality could have biased this estimate considerably. Of the methods we considered for estimating daily ration, we place most

confidence in the growth-derived estimate (that is, growth/efficiency). The independent estimates of growth rate are consistent and probably contain little measurement error, and the range of growth efficiencies we used is well within the range of estimates extant in the literature. The energy-balance estimate is minimal; but even at this feeding rate, if juvenile Atlantic menhaden depend entirely on phytoplankton they would consume a considerable fraction of estuarine phytoplankton production (see below).

Population Estimates

Food utilization rates for individual fish must be accompanied by population estimates if the importance of Atlantic menhaden in energy flow through the ecosystem is to be properly appraised. The first estimate of average population size for juveniles was derived by multiplying an estimate of average fish density, calculated for eight small estuaries (Fig. 1), by an estimate of the total habitable area along the Atlantic coast. Population size in the eight creeks during the summer was estimated from 33 separate surveys by United States Bureau of Commercial Fisheries personnel during 1957–1964 (Pacheco 1965a, 1965b, 1966). Mark-and-recapture methods were used in each creek at least 3 of the 4 years from 1961 through 1964. Populations in five of the eight creeks were estimated each of the 4 years and one (White Creek, Delaware) was censused annually from 1957 through 1964. We estimated creek areas by planimetry, using United States Coast and Geodetic Survey or United States Geological Survey maps. The geometric mean of densities of all eight streams was 1.04 fish/m². This indicator of central tendency was used because of the great variation in density among streams and the error associated with measurement of density.

The estimated average number of juveniles, 11.2×10^9 fish, is based on a mean density of 1.04/m² and a habitat of 10.8×10^9 m². This estimate of appropriate habitat, the open shoal water 2 m deep or less from the northern Massachusetts border south through Georgia (Spinner 1969), is somewhat arbitrary. Undoubtedly some juveniles occur in water deeper than 2 m and outside the given latitudinal range, but this description of habitat size generally agrees with observations of the personnel who conduct sur-

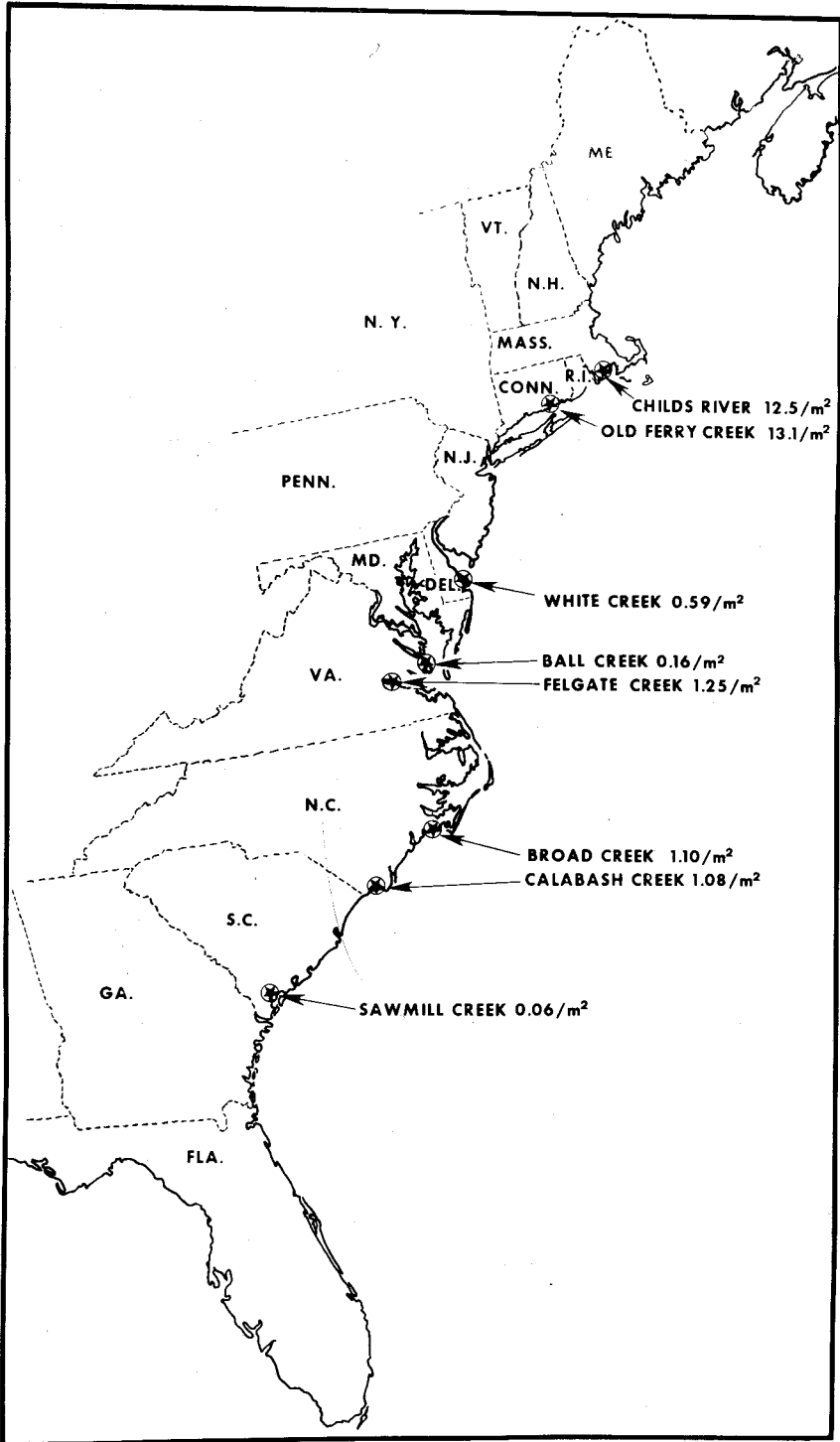


FIGURE 1.—Average abundance (numbers/m²) of juvenile Atlantic menhaden in eight eastern United States estuaries sampled from 1957 to 1964.

veys of juvenile Atlantic menhaden for the Menhaden Program of our laboratory.

We also estimated average autumn abundance of juveniles from commercial catch statistics. Staff of the Menhaden Program have compiled estimated catch by age for Atlantic menhaden since 1955. These data (Schaaf, in press) were used in a cohort analysis (Ricker 1975) to back-calculate the population of 1-year-olds in May, based on an assumed natural mortality rate of 30% per year (Schaaf and Huntsman 1972). These populations were then extrapolated back an additional 8 months to September of their birth years. For this final extrapolation we used the adult natural mortality rate, and hence obtained an average population size, perhaps conservative, of 4.4×10^9 fish.

From 1969 through 1973, our laboratory personnel tagged 81,746 juvenile Atlantic menhaden in the autumn with internal ferromagnetic tags; recoveries were obtained with magnets installed in the fish-processing plants (Nicholson 1978). Of those tagged, 502 were recovered during the same season. From these data we obtained another annual population estimate. We have assumed a 40% loss of tags due to shedding and mortality (Dean Ahrenholz, Beaufort, personal communication) and a 40% recovery efficiency of plant magnets (Kroger and Dryfoos 1972). These numbers yield two estimates of exploitation rate for 1-year-olds, depending on whether we assume the tag loss to be immediate or to occur at a constant rate throughout the time at liberty.

Let: U = exploitation rate for 1-year-olds;

N = total number tagged = 81,746;

R_1 = recoveries during first fishing season (age 0) = 502;

R_2 = recoveries during second fishing season (age 1) = 2,018;

E = plant recovery efficiency = 0.4;

S = proportion of tagged fish surviving the initial loss = 0.6;

m = monthly instantaneous natural mortality rate = $0.33/12 = 0.0275$;

x = monthly instantaneous tag loss rate due to shedding and handling mortality = $(-\log_e S)/12 = 0.0426$;

t_1 = time from tagging (September) to midpoint of fall fishery = 3.5 months;

t_2 = time from midpoint of fall fishery to

May 1 (beginning of second-season fishery) = 4.5 months.

Then, for an assumed immediate tag loss:

$$U = (R_2/E)/[(N \cdot S)\exp(-mt_1) - (R_1/E)\exp(-mt_2)] = 0.13.$$

The corresponding equation for continuous loss is:

$$U = (R_2/E)/\{N \exp[-t_1(m+x)] - (R_1/E)\} \exp[-t_2(m+x)] = 0.11.$$

In these equations we assumed that all the catch during the first year (502/0.4) was instantaneously removed on December 15, at the midpoint of the 3-month fall fishery. The 21-year average catch of 1-year-olds (949×10^9) divided by these exploitation rates gives May population estimates of 7.3 or 8.6×10^9 1-year-olds. Because tag loss probably is neither immediate nor continuous, we averaged these estimates before extrapolating them back 8 months. Hence we arrive, from tagging data, at an estimated 9.9×10^9 juveniles occupying the September estuary.

The three estimates (11.2×10^9 from survey data, 9.9×10^9 from tagging, and 4.4×10^9 from cohort analysis) are reasonably similar and, judged from catch data alone, are certainly of the correct magnitude. The total catch out of each year class from 1955 to 1975 ranged from 0.7 to 8×10^9 , and averaged 2.2×10^9 fish. This estimates the minimum abundance, as it is the number "seen," and does not account for any natural mortality during the 5 or 6 years that a cohort is in the fishery.

Population Rates of Food Utilization

From estimates of population size and food utilization rates we estimated food consumption, growth, and fecal production of all juveniles in estuaries. The amount of food consumed was calculated from individual food utilization rates (Table 1) and the average of the independent population estimates, 8.5×10^9 fish. The weight of 8.5×10^9 larvae entering estuaries is only 25,500 kg dry weight (0.003 g per fish). If, conservatively, each fish grows to 6.5 g (30 g live weight) by autumn, they would ingest $(182-278) \times 10^6$ kg of organic matter. The range in consumption figures is based on the range in growth efficiencies that were used in calculating individual consumption rates (Table 1).

Discussion

To assess the ecological impact of juvenile Atlantic menhaden, we compared the energy requirement of 8.5×10^9 juveniles to phytoplankton production, usually considered to be their main food source (June and Carlson 1971; Durbin and Durbin 1975). If it is assumed that phytoplanktonic organic matter is 50% carbon and that 150 g/m^2 of carbon are fixed annually (Thayer 1971; Williams 1973 and personal communication), then phytoplankton production in the habitat of juvenile Atlantic menhaden is $3.2 \times 10^9 \text{ kg}$. Thus the 8.5×10^9 fish consuming $(182-278) \times 10^6 \text{ kg}$ of organic matter would consume 6–9% of the annual phytoplankton production. This comparison is conservative because it does not account for any consumption by unknown numbers of juvenile Atlantic menhaden that do not survive to September. Assuming a low daily mortality rate of 0.0011, equal to the estimated value for adults (SchAAF and Huntsman 1972), would increase the food requirement by only 3%. An upper limit for daily mortality would be 0.032, which by autumn will reduce the average egg production of 54×10^{12} (Nelson et al. 1977) to our juvenile population estimate. This rate would triple the total food requirement.

As the summer progresses and the fish grow, the amount of food they consume each day increases and by fall may equal or exceed daily phytoplankton production. A population of 8.5×10^9 30-g fish (6.5 g dry weight), consuming organic matter at a rate of 13–20% of its dry weight a day, will ingest $(7-11) \times 10^6 \text{ kg/day}$. If this daily requirement were spread equally throughout the habitat, it would be $0.6-1.0 \text{ g/m}^2$, which is about the same as the average daily phytoplankton production of 0.8 g/m^2 . Of course, phytoplankton production during autumn may be somewhat higher than the yearly average, in which case the carbon fixation rate could exceed the food needs of juvenile Atlantic menhaden.

While the accuracy of these estimates is not known, it is apparent from growth data alone that the food requirement of juvenile Atlantic menhaden is large relative to estimates of estuarine phytoplankton production. When the variety of competing filter feeders, possibly including adult Atlantic menhaden, is considered, it is likely that the juveniles require more food than is temporally or spatially available to

them as phytoplankton or as components of a phytoplankton-based food web. Durbin and Durbin (1975) indicated that many of the phytoplankters in Rhode Island waters are too small to be ingested by adult Atlantic menhaden, which preferentially ingest larger particles, such as zooplankton. If juvenile Atlantic menhaden have similar feeding behavior, then some portion of phytoplankton production is unavailable to them directly. Although they may tap some of this production indirectly by ingesting phytophagous zooplankters, energy is lost in this additional conversion, which makes a complete dependence on phytoplankton production even less plausible.

One alternative energy source available to the juveniles is benthic algae. Edgar and Hoff (1976) observed adult Atlantic menhaden grazing on a thin film of benthic microalgae. In the laboratory, we observed juvenile Atlantic menhaden ingesting benthic substrate. Material that we found in field-collected juvenile Atlantic menhaden stomachs, though identified as phytoplankton (Table 1 of Peters and Kjelson 1975), also included small amounts of benthic algae (diatoms and filamentous blue-greens).

A potentially important energy source for juvenile menhaden is detritus, either filtered from the water or ingested from the sediment. In a study of the food consumed by juvenile Atlantic menhaden in Rhode Island waters, Jeffries (1975) found that although diet varied with location, it included considerable suspended organic matter (a term which includes primarily detritus, some algae, but no zooplankton). Darnell (1958, 1964) found that detritus was an important component of the stomach contents of gulf (*Brevoortia patronus*) and Atlantic menhaden. In several small samples from North Carolina estuaries, we found that detritus constituted 70% of the diet of juvenile Atlantic menhaden (Peters and Kjelson 1975). Judged from the presence of benthic algae in stomachs, some of this detritus was probably of benthic origin.

We conclude that benthic algae and phytoplankton, much of which may be too small to be consumed by menhaden, do not sustain the population of juvenile Atlantic menhaden. This conclusion is based on feeding studies and calculated food requirements. Documented cases of detrital ingestion do not prove that juveniles are dependent on detritus as food, yet the car-

bon and nitrogen content appears to be nutritionally adequate (Thayer et al. 1977). As suspended estuarine and salt marsh detritus is abundant, available, and apparently nutritious, it is likely to be a major source of food and energy. The relative importance of detritus in sustaining juvenile Atlantic menhaden may vary geographically and with fish size. However, it appears that destruction of salt marshes or other detrital sources (Gallagher 1978) in and around our estuaries could have a detrimental impact on the Atlantic menhaden population and fishery.

The arguments used in this paper demonstrate that benthic algae and phytoplankton are unlikely to be the major source of energy for the juvenile menhaden population. The converse conclusion, that detritus is an important food, cannot be demonstrated without experimental evidence showing the degree of vascular assimilation, and the relative role of the associated microflora and -fauna in menhaden energetics.

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